2.

Notes on the Functions of the Forebrain in Teleosts.

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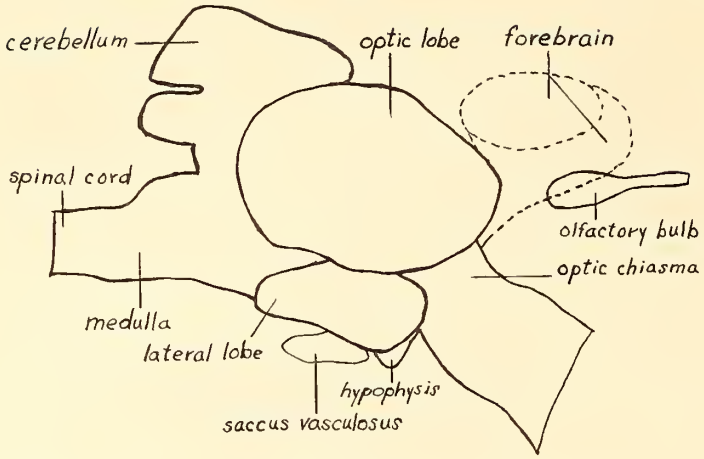
(Text-figures 1 & 2).

It has usually been assumed that the forebrain of fishes is used primarily for olfactory purposes. I wish to submit a report of some observations which, together with others recently published, suggest that the specialized forebrains of some fishes may be of importance for other purposes as well.

In the course of carrying out some experimental studies on the optic system of fishes at the Bermuda Biological Station it occurred to me to make lesions in the forebrains of a few species. The primary object of such lesions was to secure degeneration of fiber tracts arising in the forebrain. Anatomical investigations in one species, *Holocentrus ascensionis* (Osbeck), have revealed an elaborately organized telencephalon intimately connected by large and small bundles of fibers with other parts of the brain. In view of the complexity of this brain and in view of the current interest in the functions of the teleostean forebrain it seems worth while to summarize here the observations recorded in my protocols. The latter include notes on normal control animals, on individuals with one or both eyes enucleated, and on individuals with forebrain lesions.

The specimens of *Holocentrus* used ranged from 8 to 12 cm. in length. These squirrel-fish live very well in aquaria provided with running salt water and they withstand operative interference readily. For all operations they were anaesthetized by immersion in a solution of 1 part chloretone in 4,000 parts of sea water. They were then held in a damp cloth while a segment of the dorsum of the skull was removed to expose the forebrain. One or both hemispheres were extirpated or isolated lesions were produced. When the animals were replaced in sea water, they quickly recovered from the anaesthesia. At first it was thought necessary to close the skull opening with some inert substance but such efforts were abandoned when the substances used failed to adhere and the animals showed no ill effects from the exposure of the brain. At no time was there evident any disturbance which could be attributed to the direct bathing of the brain by the sea water. Granulation tissue growing in from the periphery gradually filled the wound. After 54 to 61 days the fishes were decapitated and the heads were prepared for microscopic study to provide controls of the location and the extent of the lesions and to permit investigations of the degenerated fiber tracts. These preparations have shown that the lesions intended were made. In some cases the total forebrain, with the exception of the sessile olfactory bulbs, was removed. The figures illustrate such a case.

A description (with figures) of the gross appearance of the brain and



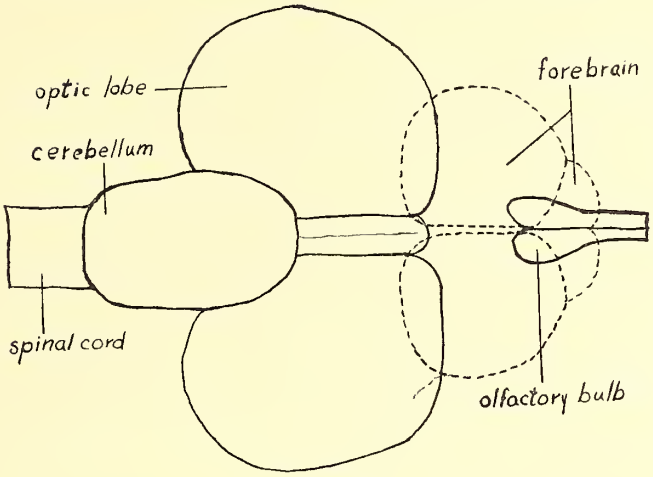
Text-fig. 1.

Outline sketch of a lateral view of the brain of *Holocentrus*. The tissue removed in the most radical operations is indicated by broken lines. ×8.

of the anatomy of the optic system of this fish has previously been presented by the author (1). A short account of the normal behavior of *Holocentrus* was included, emphasizing the importance of vision in the life of this large-eyed, nocturnal teleost. In the aquarium, as in its natural habitat, it prefers the darker corners and recesses where during the daytime it lies more or less quiescent in the shadow of a rock. At dusk and after dark, and in dim light generally, it swims about more freely. For a few days after being placed in an aquarium most individuals remain in concealment and are with difficulty enticed into the open to feed. They notice food only when it is in motion and if anything prevents them from seeing it or securing it before it comes to rest, it will remain untouched. If food is dropped close to the place of concealment, it is usually seized in midwater. There is a notable absence of the investigative nibbling characteristic of so many fishes. In the course of a few days it is possible to induce them to leave their hiding places and come to the surface to take food from forceps or fingers. Inimical visual stimuli generally elicit the sudden erection of the rather large and spiny dorsal fin, a reaction which is usually followed by flight and concealment.

All of this behavior is modified in totally blinded individuals. They are less active and they are indifferent concerning the part of the aquarium they occupy. They tend to find some vertical surface against which they lean as they rest on the bottom. Food is found only with great difficulty even when it is placed close to the mouth or olfactory pit. Blinded fishes are excited by the proximity of food but are unable to localize it accurately enough to obtain it without aid. They react slowly and briefly to an object moving in the water close to the body but their dorsal fins are seldom erected except by direct tactile stimuli.

Individuals blind on one side only illustrate even more strikingly the importance of vision to the squirrel-fish. Their activity is as great as that of intact animals and they respond to visual and tactile stimuli (including movements of objects in the water) presented on the intact side in the same way that normal fishes do. To tactile stimuli presented on the blind side, however, the reaction has a much higher threshold and the flight response is less both quantitatively and in temporal persistence. Such an observation



Text-fig. 2.
Outline sketch of a dorsal view of the brain of *Holocentrus*, showing the area extirpated (in broken lines). ×8.

leads one to suspect that the more lively response obtained from supposedly tactile stimuli presented on the normal side is really due to visual cues. The normal dorsal fin erection and flight response occur even when stimuli presented on the intact side are separated from the body of the fish and from the water by the untouched glass walls of the aquarium.

In no case did partial or complete removal of the forebrain of *Holocentrus* have any apparent effect upon the elements of behavior noted above for the normal control animals. The operated individuals were just as active as the latter, reacted to feeding stimuli in the same way and could be trained to take food from my fingers. They reacted to inimical stimuli with a similar fin and flight response. When normal and operated individuals occupied the same aquarium, their only distinguishing characteristic was the head wound.

It is surprising that *Holocentrus*, provided with such a specialized forebrain, from the anatomical point of view, exhibits so little disturbance of normal behavior when the forebrain is removed. Other investigators (2) have found that decerebration of teleosts is followed by deficits in olfaction, in schooling reactions (3, 4), in breeding behavior (5), and by a rise in the stimulus threshold (6). A restriction to purely reflex types of response has also been noted (6).

It may be that the difference between my observations and those of others can be explained in part by the differences in the habits of the species studied and in part by the adequacy of visual reflexes to carry out the solution of all problems met by the squirrel-fish in uncomplicated aquarium life. Olfaction is relatively unimportant to it but an olfactory deficit would very probably be revealed by more refined methods of testing. Chemical cues alone were not sufficient for finding food, as they are for many other forms, whereas vision unaided by olfaction enabled the fishes to feed normally.

Very little is known of the social behavior of *Holocentrus*. Although it is a relatively individualistic fish, it does "school" on occasion. Mr. Louis Mowbray, Director of the Bermuda Aquarium, has told me that there is a seven-year cycle in the abundance of the squirrel-fishes in Bermuda waters.

At the times of great abundance these fishes swim along the shores in large schools. Under these conditions decerebrate forms might exhibit a deficit not otherwise evident.

Inasmuch as the breeding habits of the squirrel-fishes are also unknown, it is obvious that this aspect of their social behavior cannot well be tested. It is possible that refined methods of investigation, such as those used by Hosch, would reveal some rise in the threshold of stimuli and some change in the patterns of response.

The observations here reported, as well as many others, indicate that the problem of the function of the forebrain in fishes has many complications. There is probably as great a variation in the cerebral physiology of the teleosts as in their cerebral anatomy. No other comparably limited group of vertebrates exhibits so wide a diversity of morphology in its nervous system. In this group, also, are to be found equally wide variations in behavioral habits, which are an expression of neural physiology. The observations made on one form, therefore, cannot safely be generalized to apply to all forms. Careful studies must be made on many different species if we are to arrive at reliable conclusions.

In the meantime, it should not be surprising that different species of fishes studied under different conditions (often those which are decidedly artificial) by different investigators appear to have varying deficits after forebrain extirpation. The work of previous investigators suggests that the forebrain may have many functions which vary in importance in the different fishes. For those species with relatively poor visual or tactile senses the olfactory function may be paramount. For those that normally swim chiefly in groups the forebrain may supply the necessary coordination. For those with other elaborate social behavior characteristics, such as specialized breeding and brooding habits, it may provide the integration of sensory stimuli to produce the customary pattern of reproductive activity; and its massive fiber tract connections with the hypothalmus may possibly influence reproduction through the effect of stimuli on the hypophysis. In many cases it may prove to be true that the forebrain of teleosts, like that of higher vertebrates but to a lesser degree, is an integrative center capable of giving rise to non-stereotyped responses appropriate to the stimuli received. All of these functions, and many others, may be present to varying degrees in all fishes and yet not be evident in an experimental analysis because of inadequate methods of testing or because their expression is masked by more prominent behavioral traits. If, however, one dares to predict physiology from anatomy, then the known anatomical variations in cellular distribution and in the fiber pathways relating the cells indicate a diversity of function of the forebrain in different groups of fishes.

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